POPULATION AND SITE CHARACTERISTICS OF A RECENTLY DISCOVERED DISJUNCT POPULATION OF *CROTON ALABAMENSIS* (EUPHORBIACEAE)

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ABSTRACT

A disjunct population of *Croton alabamensis* E. A. Smith ex Chapman, a Category 2 Candidate species being considered for addition to the List of Endangered and Threatened Plants, was discovered over 1000 km from any previously known population. This paper describes the extent and status of this disjunct population. The *Croton* population is situated along canyon bottoms and appears healthy and self-sustaining. *Croton* occurrence exhibits no association with overstory gaps, disturbance, or particular fluvial geomorphic features. The species appears to be restricted to canyon bottoms characterized only by mesic conditions provided by the presence of overstory cover and deep soils. Differences between the ecology of this newly discovered population and those of the heretofore considered endemic Alabama populations are discussed.

RESUMEN

Una población alopátrica de *Croton alabamensis* E. A. Smith ex Chapman, Categoría 2 de Especie Candidata, que está siendo considerada para ser agregada a la Lista de Plantas en Peligro de Extinción, fue descubierta a una distancia de 1000 km de la población previamente conocida. En este trabajo se describe la extensión y estado de la población alopátrica. La población de *Croton* esta situada a lo largo del fondo de un cañon aparentando poder sobrevivir y crecer en buenas condiciones. La ocurrencia de *Croton* no parece tener asociación con espacios desnudos, perturbaciones o características fluviales geomórficas

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particulares. La especie parece estar restringida al fondo del cañon caracterizado solamente por condiciones mesomórficas debidas a la presencia de cobertura y suelos profundos. Las diferencias entre las características de esta población recientemente descubierta y las de población heterofítica en Alabama, antes considerada endémica, son discutidas.

INTRODUCTION

Croton alabamensis E. A. Smith ex Chapman (Euphorbiaceae) has been described as "one of the rarest shrubs in the United States" (Farmer and Thomas 1969). It is a short-lived ($<$20 y), multi-stemmed, monoecious shrub $<$3 m tall found primarily on limestone and shale outcrops along the Warrior and Cahaba Rivers, Tuscaloosa and Bibb counties, Alabama. It was collected once in 1899 in Tullahoma, Coffee County, Tennessee, but has not been reported from there subsequently. *Croton alabamensis* has long been thought to grow only in isolated populations within these two neighboring counties. Due to its restricted range, it is being considered for addition to the List of Endangered and Threatened Plants under the Endangered Species Act of 1973, as amended. It currently is designated as a Category 2 Candidate, which means that "there is some evidence for vulnerability, but ... there are not enough data to support listing proposals at this time" (USDI 1991).

In early 1990, *Croton alabamensis* was discovered over 1000 km from any previously known population on the U.S. Army's Fort Hood, Texas. The population was discovered by John Cornelius, a wildlife biologist with the Fort Hood Resource Management Department, during an excursion to view bird habitat in the Owl Creek Mountains. Cornelius showed the population several weeks later to Carol Beardmore of the U.S. Fish and Wildlife Service and Rex Wahl of Texas Parks and Wildlife. Ginzbarg (1992) mistakenly credited the discovery to Beardmore and Wahl. Not long afterwards, a second and a third population were discovered in Travis County, to the south. The species identity was determined by Steve Ginzbarg, a graduate student in botany at the University of Texas, Austin. Ginzbarg (1992) subsequently determined that the Texas plants are sufficiently distinct to merit varietal status. He consequently described them as *Croton alabamensis* E. A. Smith ex Chapman var. *texensis* Ginzbarg (Ginzbarg 1992). Key characteristics of the Texas variety are represented in Figures 1 and 2.

In June 1991, we undertook to describe the extent and status of the population at Fort Hood as part of the Department of Defense's Legacy Resource Management Program. The Legacy Program was established to enhance conservation of biologically and culturally significant resources on military lands. Our study is aimed at gathering the requisite information to effect proper stewardship of this species at Ft. Hood. We therefore restricted our analysis to only one of the three Texas populations (i.e. the Ft. Hood population). We recommend that similar studies be undertaken in both

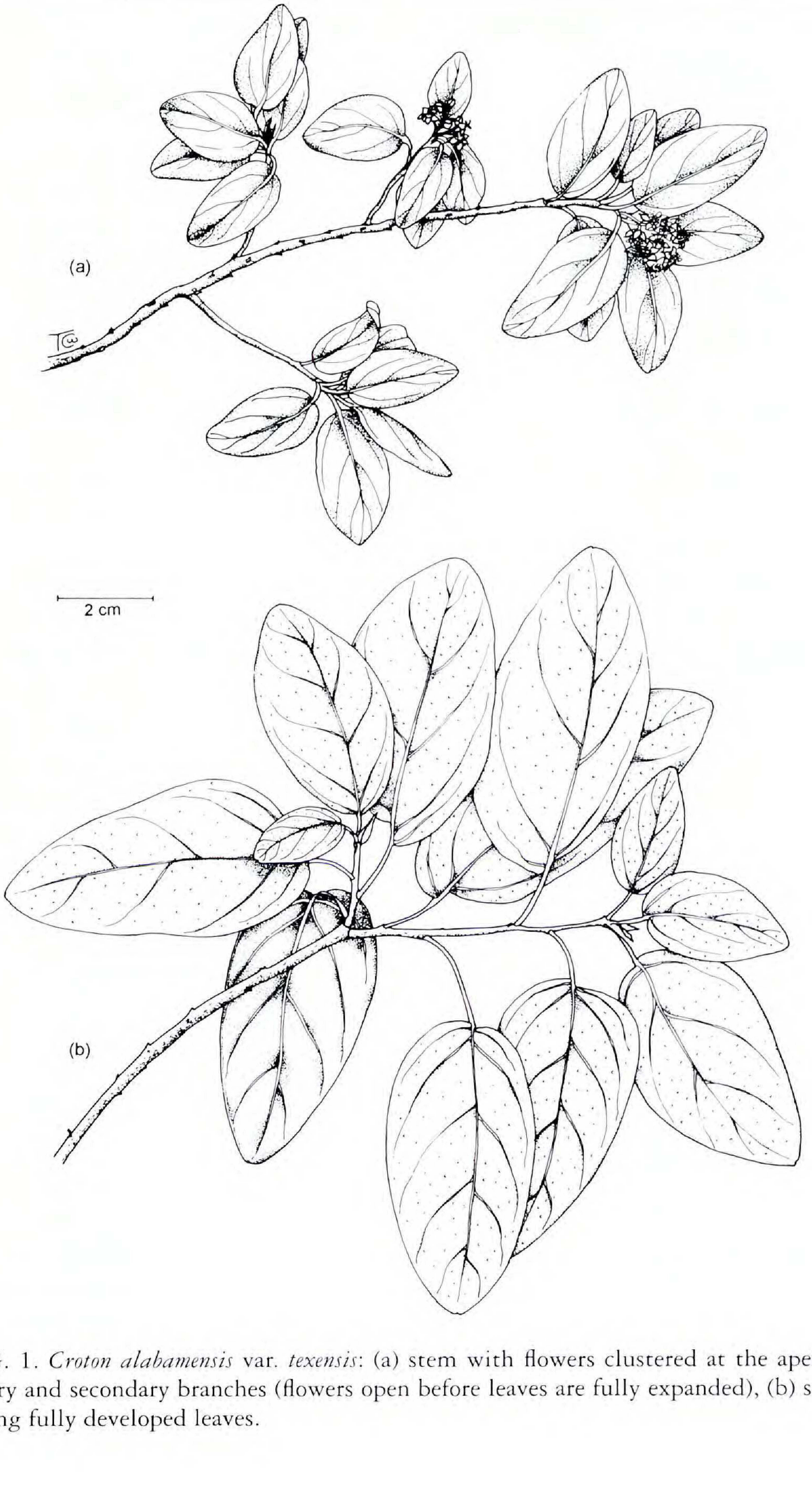

FIG. 1. *Croton alabamensis* var. *texensis*: (a) stem with flowers clustered at the apex of primary and secondary branches (flowers open before leaves are fully expanded), (b) stem showing fully developed leaves.

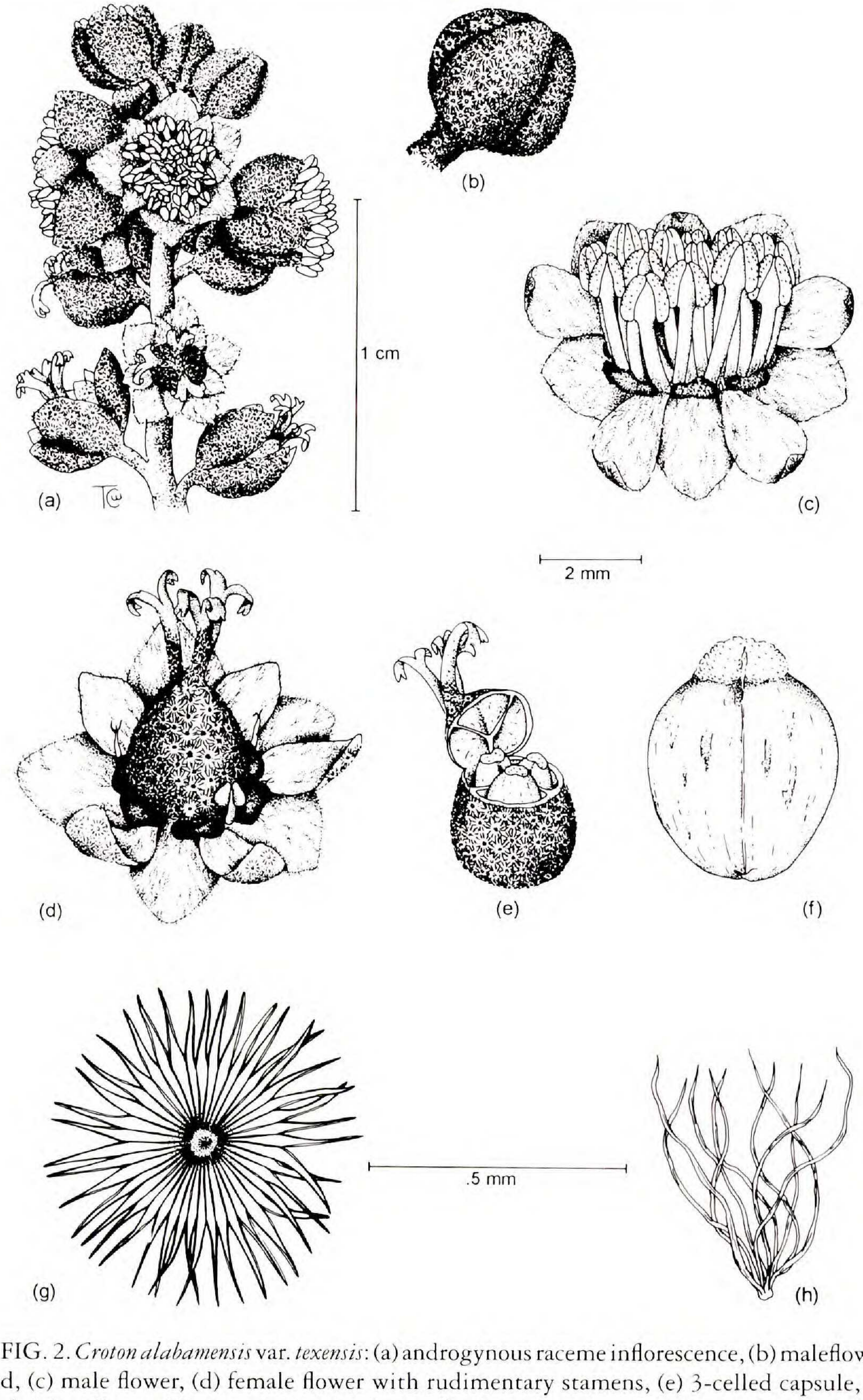

FIG. 2. *Croton alabamensis* var. *texensis*: (a) androgynous raceme inflorescence, (b) maleflower bud, (c) male flower, (d) female flower with rudimentary stamens, (e) 3-celled capsule, (f) seed, (g) stellate trichome common on leaves, buds, and ovary, (h) trichome found on disk lobes of male and female flowers.

Texas and Alabama to assess the status of all populations of this rare and scientifically important species.

STUDY AREA

This study was conducted in several small watersheds of the Owl Creek Mountains, Bell and Coryell counties, in the Hill Country of central Texas (31°N, 97°W). The Owl Creek Mountains (elevation ~300 m) are composed of Mesozoic limestone overlain by clayey and loamy soils (McCaleb 1985). The formation rises to its summit plateau ~65 m above the west-to-east flowing Owl Creek in less than 2 km. Intermittent tributary streams run northward to the creeksuch that virtually all canyon walls have east- and west-facing aspects.

The climate is hot in the summer, and the winters are generally mild, with an occasional cold surge. The average daily temperature during the summer is 28°C, with an average daily maximum of 36°C. Winter daily temperatures average 9°C, with an average low of 3°C. Rainfall is distributed uniformly throughout the year, with a slight peak in the spring and an average annual total of 825 mm (McCaleb 1985). Owl Creek flows to some extent throughout the year, but the tributary streams are dry most of the year.

The vegetation of the area (see Appendix 1 for complete plant species list) is primarily Ashe juniper (*Juniperus ashei* Buchh.) woodland of the appropriate character to meet the habitat needs of two rare birds, the black-capped vireo (*Vireo atricapilla*) and the golden-cheeked warbler (*Dendroica chrysoparia*). The vireo primarily inhabits the shrubby balds of the summit plateau, but the warbler requires the bark of relatively old junipers for nesting materials and mature hardwoods for feeding (J. Cornelius pers. comm.).

Prior to our study, *Croton alabamensis* var. *texensis* had been identified from two of the tributary canyons of Owl Creek. We searched five additional canyons and found only three more plants in the canyon between the original two and several plants along the stretch of Owl Creek between the two tributaries; populations of *Croton* appear to be largely restricted to the two original canyons. Our study involved two phases: a description of the structure and habitat of the two *Croton* populations (canyons 1 and 3) and an attempt to discern why *Croton* is all but absent from the canyon between (canyon 2). Subsequent to the completion of this study, another population consisting of 35 individuals was located in a canyon three km east of the study area. This population is not considered in our analysis.

METHODS

The bed of each of the three canyons was mapped using a tape and a hand-held compass. The slope of the creek was measured using a hand-held clinometer. Three high density stands of *C. alabamensis* var. *texensis* were identified for intensive sampling along the creekbeds in Canyons 1 and 3. At each sample location, two transects were established perpendicular to the creekbed to facilitate sampling of both east- and west-facing aspects. In Canyon 2, which lacked *Croton*, similar pairs of transects were established at distances up the canyon comparable to those identified in Canyons 1 and 3.

Slope topography, overstory and understory cover, *Croton* seedling density, *Croton* adult population structure, and soil depth were determined along each transect. At each site, a tape was stretched upslope beyond the extent of the *Croton* population. In some cases, this was as far as 60 m from the creekbed, but was generally less. Transects in Canyon 2 were 30–40 m long. Slope breaks and important topographic features were noted along the slope, and a cross-section map was prepared for each transect. Soil depths were measured at 10 m intervals and at important topographic features by probing the soil with a 1 m rod.

Along the tape, cover of overstory (>2 m tall) and understory (<2 m but >10 cm tall) vegetation was determined using the line-intercept method (Mueller-Dombois and Ellenberg 1974). The line also served as the center of a 2 m wide *Croton* seedling belt in which individuals <30 cm tall were tallied.

Croton >30 cm tall were sampled using a modified nearest-neighbor method adapted from those described by Mueller-Dombois and Ellenberg (1974). Starting at the beginning of the line (middle of the creekbed), a 180° arc was searched upslope for an individual of *Croton* >30 cm tall. The distance and azimuth to the nearest plant were recorded as were the height of the tallest shoot and the diameter of each live shoot (to the nearest 0.5 cm). From that plant, the process was repeated until no plants could be found within 10 m of the last plant (Fig 3). In only one case, the process was suspended and moved back to the tape when the search led to a plant >10 m from the tape. Thus, all plants were sampled within 10 m of the tape.

Consistent with other nearest-neighbor methods, the distance between plants was assumed to be related to the share of the total area allotted to an individual plant. From these data, population density could be calculated as the total number of plants sampled divided by the sum of areas allotted to individual plants. Additionally, using a simple trigonometric conversion, the density represented by individual plants could be plotted against distance from the creek to assess changes in density related to environmental variables.

Sizes of individual, multi-stemmed *Croton* plants were described using the statistic of equivalent diameter (D_{eq}). Equivalent diameter is the diameter of a single stem that possesses the same cross-sectional area as the sum of all the stems borne by the plant. For example, as the total cross-sectional area of four shoots, each 2 cm in diameter ($4 \times 3.14\ cm^2$) is equal to that of one shoot, 4 cm in diameter ($12.56\ cm^2$), the D_{eq} for the four shoots is 4 cm.

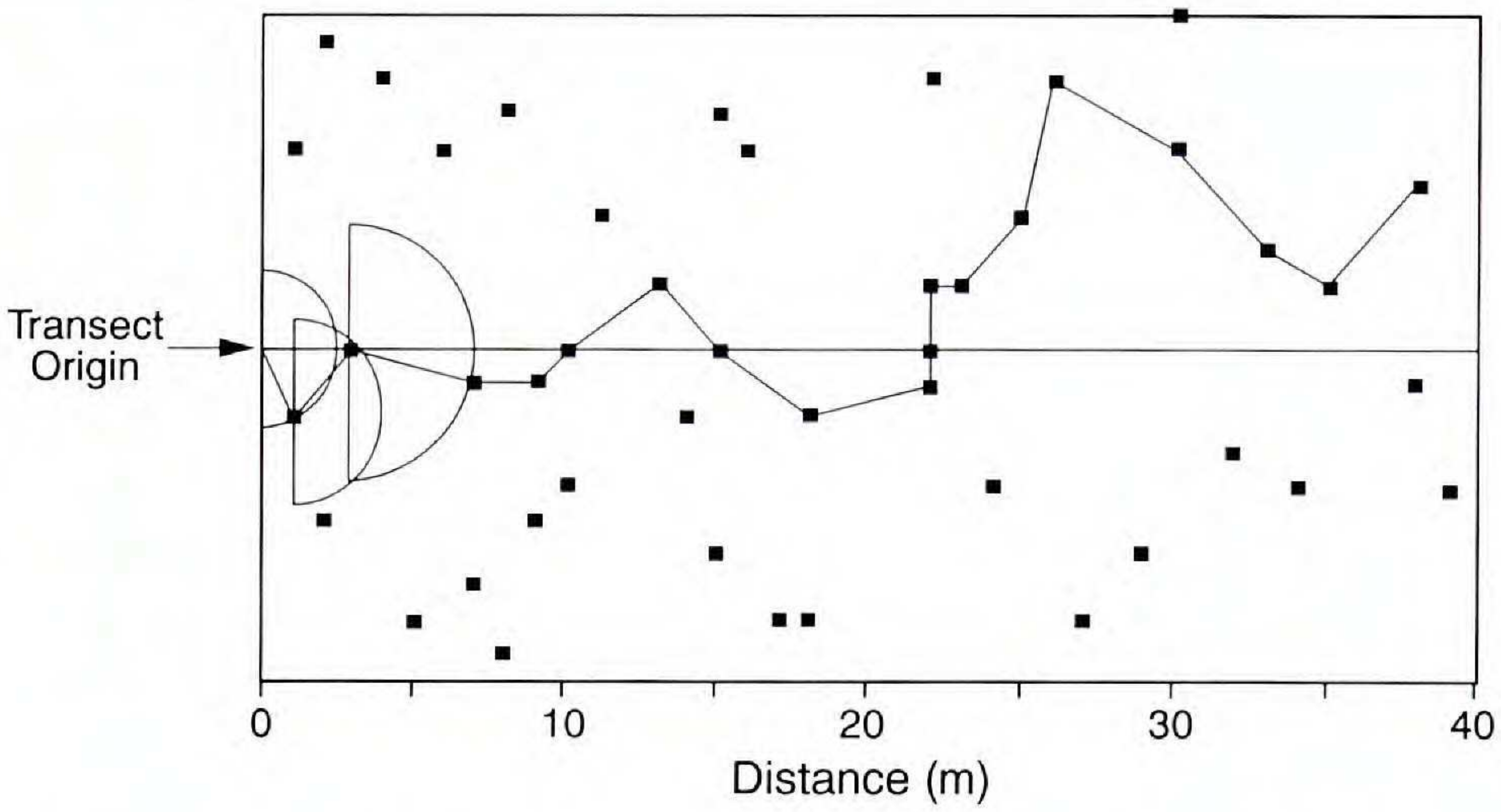

FIG.3. Illustration of the modified nearest neighbor method for sampling *Croton* height, and diameter and calculating density. Solid squares indicate plant locations within a hypothetical transect. Solid squares connected by line indicate sampled plants.

RESULTS

Autecology

The population structures of *Croton alabamensis* var. *texensis* in the two canyons are presented in Figure 4. In both canyons, *Croton* was well represented in the smaller diameter classes, but also occurred as large mature plants. This decreasing monotonic population structure was found in all transects in which *Croton* was relatively dense. Therefore, both canyons appeared to support healthy populations of adults, juveniles, and new recruits.

Croton density was highly variable within Canyons 1 and 3. Each canyon contained places in which scarcely an individual was found. In other places, *Croton* formed dense thickets in which it dominated to the near exclusion of other understory species. The densest stands occurred in Canyon 1 where *Croton* density (adults and seedlings) in two transects exceeded 100 plants/100 m^2, but three transects in Canyon 3 exceeded 50 plants/100 m^2 (Table 1). Overall, we estimate the number of plants occurring in the 1.5 km of creekbed in Canyons 1 and 3 to be ~20,000 individuals.

In general, *Croton* was found only in the canyon bottoms. No individuals were found >60 m from the creek, and of the 12 transects containing *Croton*, only four contained plants >40 m from the creek. *Croton* density fluctuated, but *Croton* did not decline proportionally with distance from the creek.

Canopy gaps along the line intercept showed no correlation with *Croton* occurrence. *Croton* were found in openings and in the deepest shade. The canyons of the Owl Creek Mountains have been subjected to harvesting of juniper trees for fence posts, and some of the gaps may have been anthropogenic.

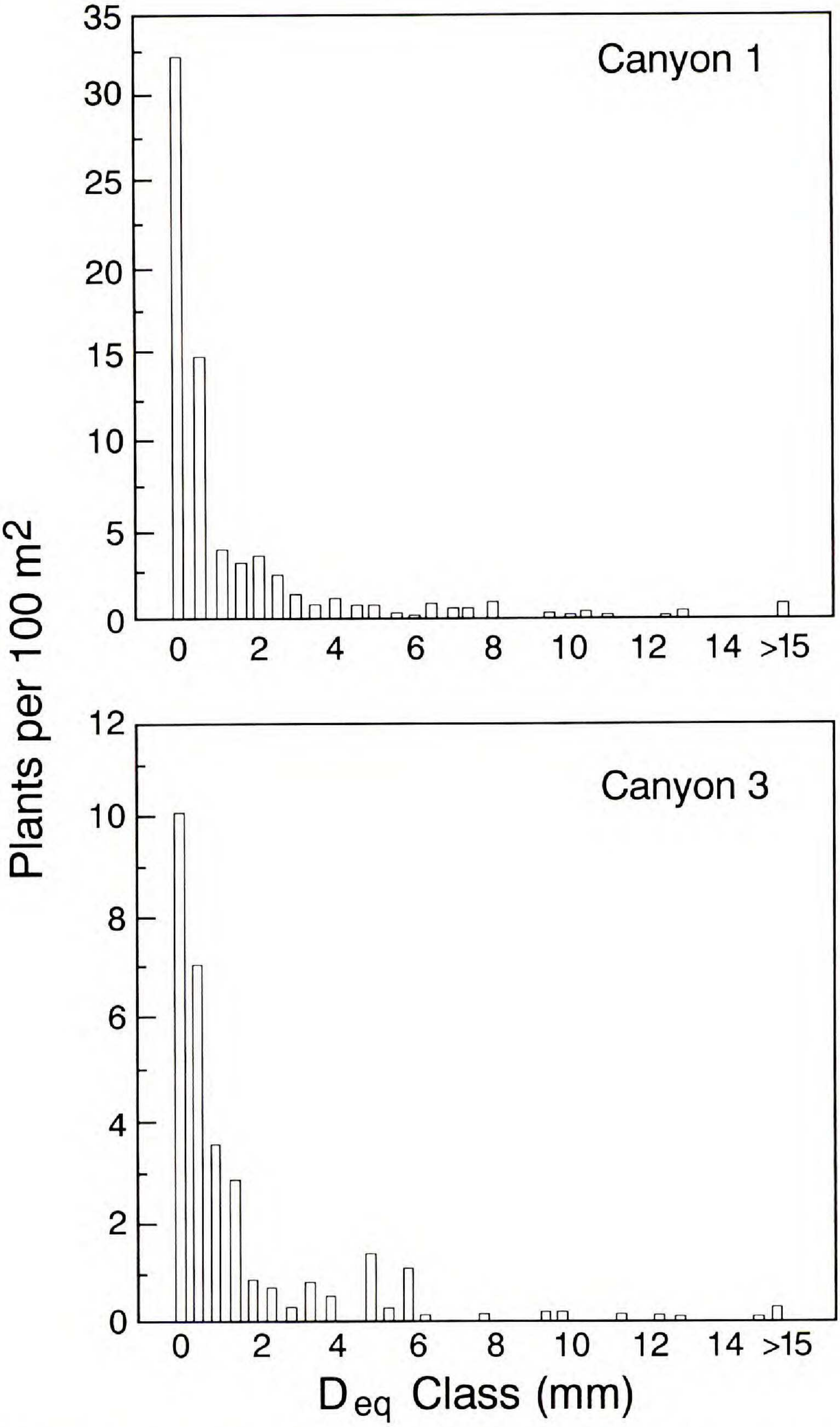

FIG. 4. *Croton* population size structures, indicating number of plants by equivalent diameter (D_{eq}) class. See text for explanation.

TABLE 1. Characteristics of the 18 transects.

		VEGETATION COVE					CROTON	
Canyon	Tran	>2m (%)	<2m (%)	Slope (%)	Aspect	Watershed Size (ha)	Density (#/100m^2)	
1	1	77	21	16.7	E	1400	16.2	23.2
1	2	85	37	30.0	W	1400	46.8	61.2
1	3	69	18	16.7	E	925	5.1	28.2
1	4	50	39	10.0	W	925	13.1	12.6
1	5	75	50	18.3	W	800	98.6	91.0
1	6	94	38	33.3	E	800	13.0	18.2
2	1	74	16	53.3	W	425	0	0
2	2	77	25	16.7	E	425	0	0
2	3	90	37	33.3	E	375	0	0
2	4	52	39	13.3	W	375	0	0
2	5	75	42	53.3	E	325	0	0
2	6	66	37	30.0	W	325	0	0
3	1	89	23	25.0	E	600	2.1	13.4
3	2	84	49	10.0	W	600	2.0	4.4
3	3	96	54	60.0	E	350	9.7	55.8
3	4	99	30	21.7	W	350	23.1	19.9
3	5	99	47	30.0	W	325	23.4	28.6
3	6	77	39	60.0	E	325	0	2.1

In some cases, the loggers incidentally cut adult *Croton* along roads and skid trails, but the plants sprouted and were growing well.

Topographic features also showed no direct correlation with *Croton* density. *Croton* occurred on bank slopes, terraces, and on toeslopes of each canyon. Soil depth, however, explained much of the variability in *Croton* distribution. A comparison of soil depth with the presence of *Croton* along the transect indicated a significant association of adult plants with deep soil ($p<0.05$; Kruskal-Wallis test). Our inability to measure depths in excess of 1 m means that the measured mean soil depth in the presence of *Croton* (0.80 m; $n=64$) was probably considerably less than the true mean. In contrast, soil measurements in the absence of *Croton* averaged only 0.42 m ($n=33$) in Canyons 1 and 3.

Comparison of *Croton* density with overstory species composition suggests an association with mesic sites, as would be expected from the observed restriction of *Croton* to the canyon bottoms. Figure 5 shows the relationship of adult *Croton* density to the combined cover of *Fraxinus texensis* (Gray) Sarg. and *Quercus muhlenbergii* Engelm. and to the combined cover of *Juniperus ashei* and *Quercus texana* Buckl. within 40 m of the creek. These four species dominated the overstory stratum in these canyons; only the woody vine *Vitis mustangensis* Buckl. contributed comparable cover over the study area. Of the

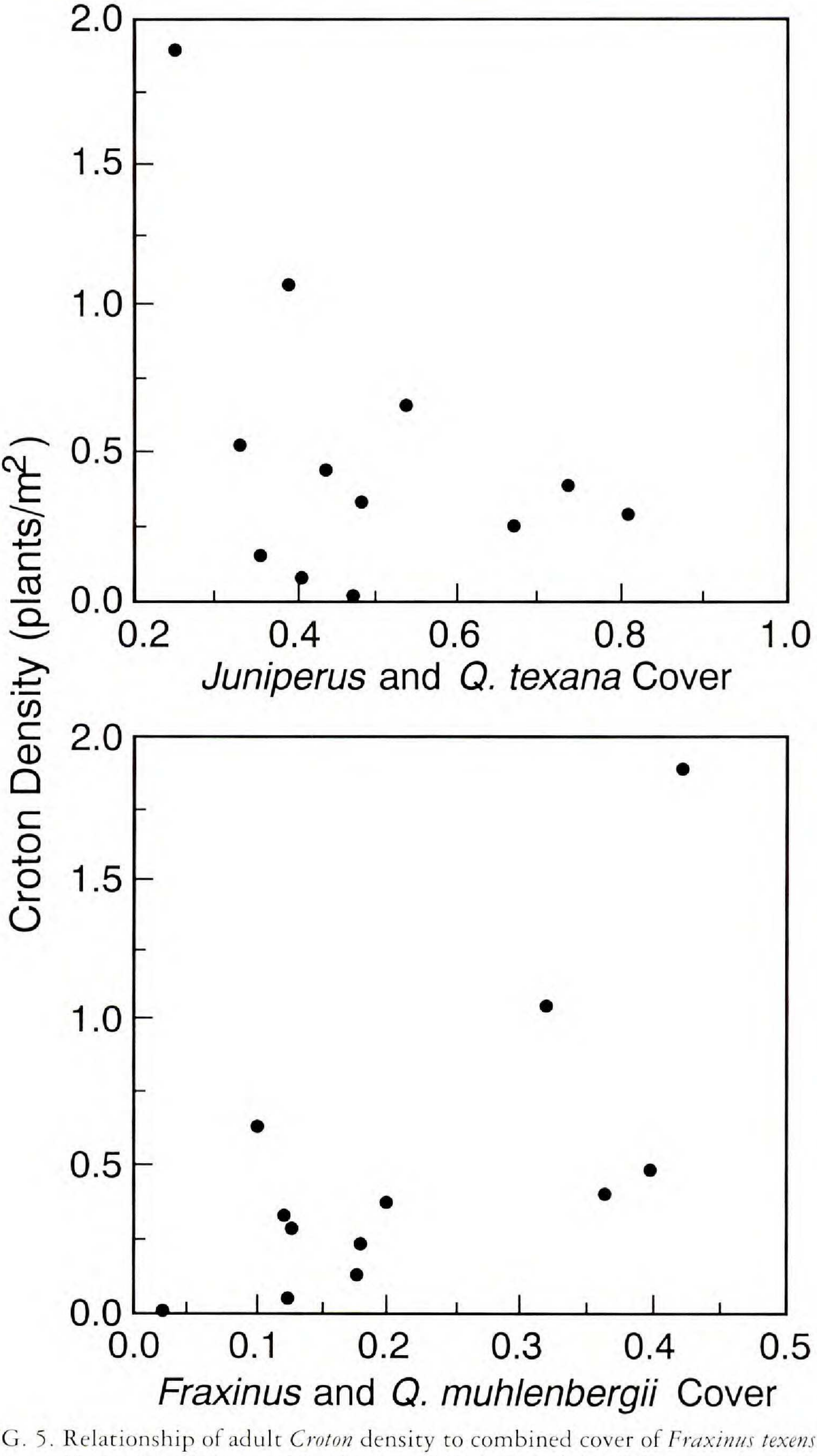

FIG. 5. Relationship of adult *Croton* density to combined cover of *Fraxinus texensis* and *Quercus muhlenbergii* and the combined cover of *Juniperus ashei* and *Quercus texana*.

three species of oak encountered during sampling, *Q. muhlenbergii* is the most mesic (Miller and Lamb 1985), and *Fraxinus* is found primarily in canyons (Correll and Johnston 1970). *Juniperus* is not so restricted, and *Q. texana* is described as occurring on "dry limestone hills and ridges" (Miller and Lamb 1985). In the study area, *Croton* was more abundant on mesic transects in which *Fraxinus* and *Q. muhlenbergii* were common and less abundant on dry transects in which *J. ashei* and *Q. texana* were most common.

Synecology

The four tree species listed above dominated the vegetation of all three canyons. Figure 6 shows the contribution of these species to the overstory cover within 40 m of the creek (40 m was used as the limit of *Croton* habitat). The dominant species in all three canyons was clearly *J. ashei*, which contributed about one-third of the cover. The other three species collectively contributed another third. These four were the only species to contribute >10% relative cover in one of the three canyons, although some species, such as *V. mustangensis*, *Ulmus crassifolia*, Nutt. *Juglans major* (Torr.) Heller., and *Celtis laevigata* Willd. were abundant locally (Appendix 2). All overstory species contributing <10% relative cover are included in Figure 6 as "minor species."

In an attempt to discern differences in habitat characters between the canyons supporting *Croton* populations and Canyon 2, we subjected transect cover data to principal components analysis (PCA) (SAS/STAT User's Guide 1988). If the transects in Canyon 2 differed in overstory composition from the other two canyons, those sites would have segregated as a distinct habitat type. Canyon 2 showed no difference in habitat from the other two as expressed in overstory composition (Fig. 7).

Likewise, understory cover displayed no pattern related to *Croton* occurrence. With the exception of *Croton* itself, all three canyons supported similar understory communities (Appendix 2). In the two canyons in which it occurred, understory *Croton* cover averaged 10.4%. (Again, placement of the transects was biased by the presence of dense populations.) Other relatively abundant understory species included *Fraxinus* species (5.5%), *V. mustangensis* (3.9%), *Rhamnus caroliniana* Walt. (3.4%), *J. ashei* (3.2%), *Rhus toxicodendron* L. (2.6%), various grasses (2.4%), *Q. texana* (2.1%), and *Ilex decidua* Walt. (2.0%).

The three canyons differed very little in both total overstory and understory cover. Overstory cover ranged from 50% in one transect in Canyon 1 to 99% in two transects in Canyon 3, but no significant difference occurred among canyons (Table 1). Similarly, understory cover ranged from 16% in one Canyon 2 transect to 54% in a Canyon 3 transect, but canyon means were similar.

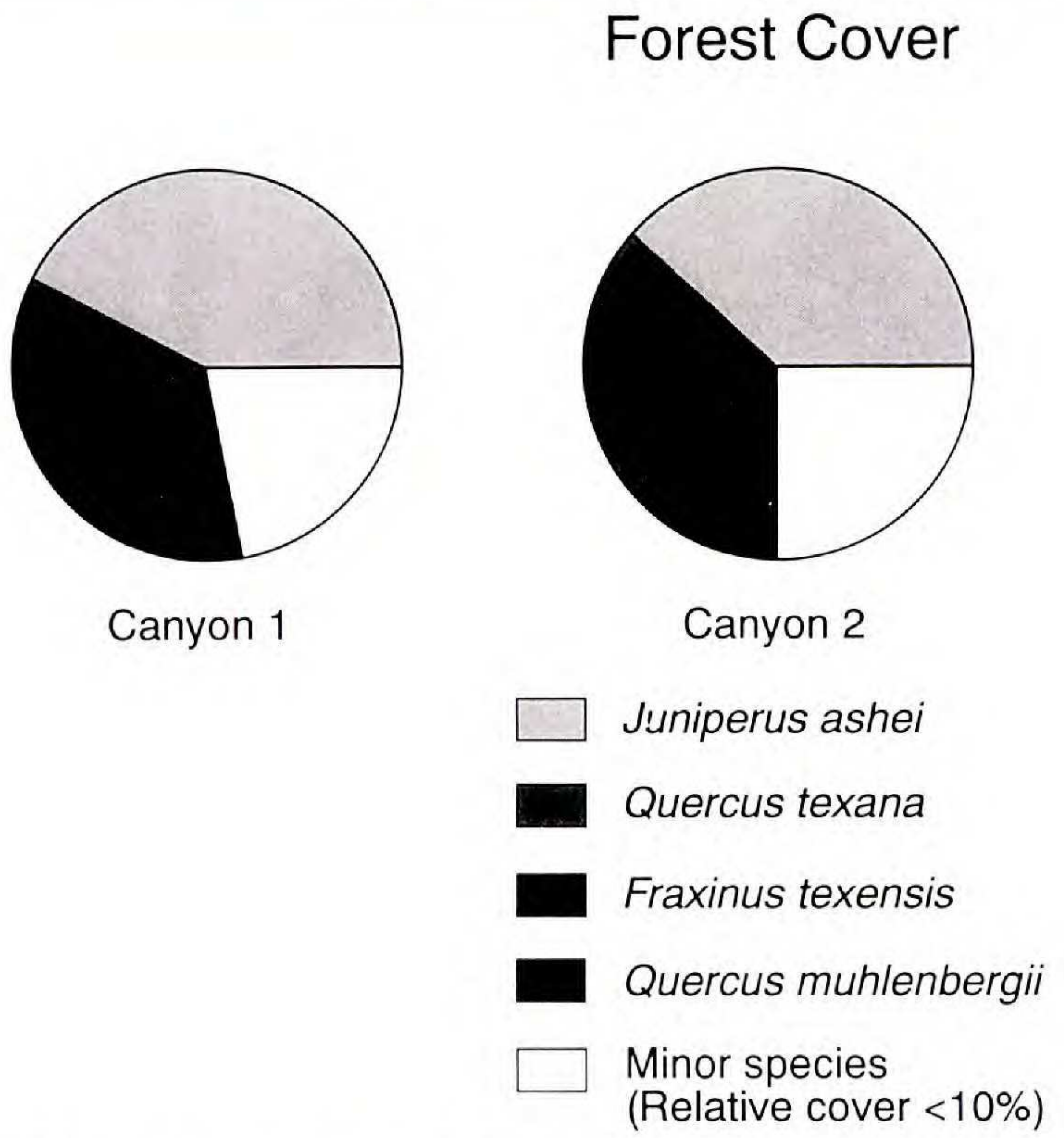

FIG. 6. Relative cover of the four dominant overstory species. All overstory species contributing <10% relative cover are included as "minor species."

Steepness of canyon walls within 40 m of the creek varied widely from site to site (10% to 60%), but means from the three canyons were similar (Table 1). Canyons 1 and 3 were the largest watersheds, but watershed areas above *Croton* populations in Canyon 3 were no larger than those present in Canyon 2. Likewise, soils of a depth that favored *Croton* in Canyons 1 and 3 were abundant in Canyon 2. The only morphological feature distinguishing Canyon 2 from Canyons 1 and 3 was the steepness of the creekbed. Streambed gradient in Canyon 2 (3.81%) was significantly steeper than in Canyons 1 and 3 (1.92% and 2.11%) ($p<0.05$; Kruskall-Wallis test).

DISCUSSION

Croton alabamensis var. *texensis* in the Owl Creek Mountains grows in healthy, self-sustaining populations along the bottoms of tributary canyons and the connecting section of Owl Creek. *Croton* occurrence exhibits no association with overstory gaps, disturbance, or particular fluvial geomorphic features. It appears to be restricted to canyon bottoms characterized only by mesic conditions provided by the presence of overstory cover and deep soils. There is some suggestion that high cover of *F. texensis* and *Q. muhlenbergii* indicates a good site for *Croton*.

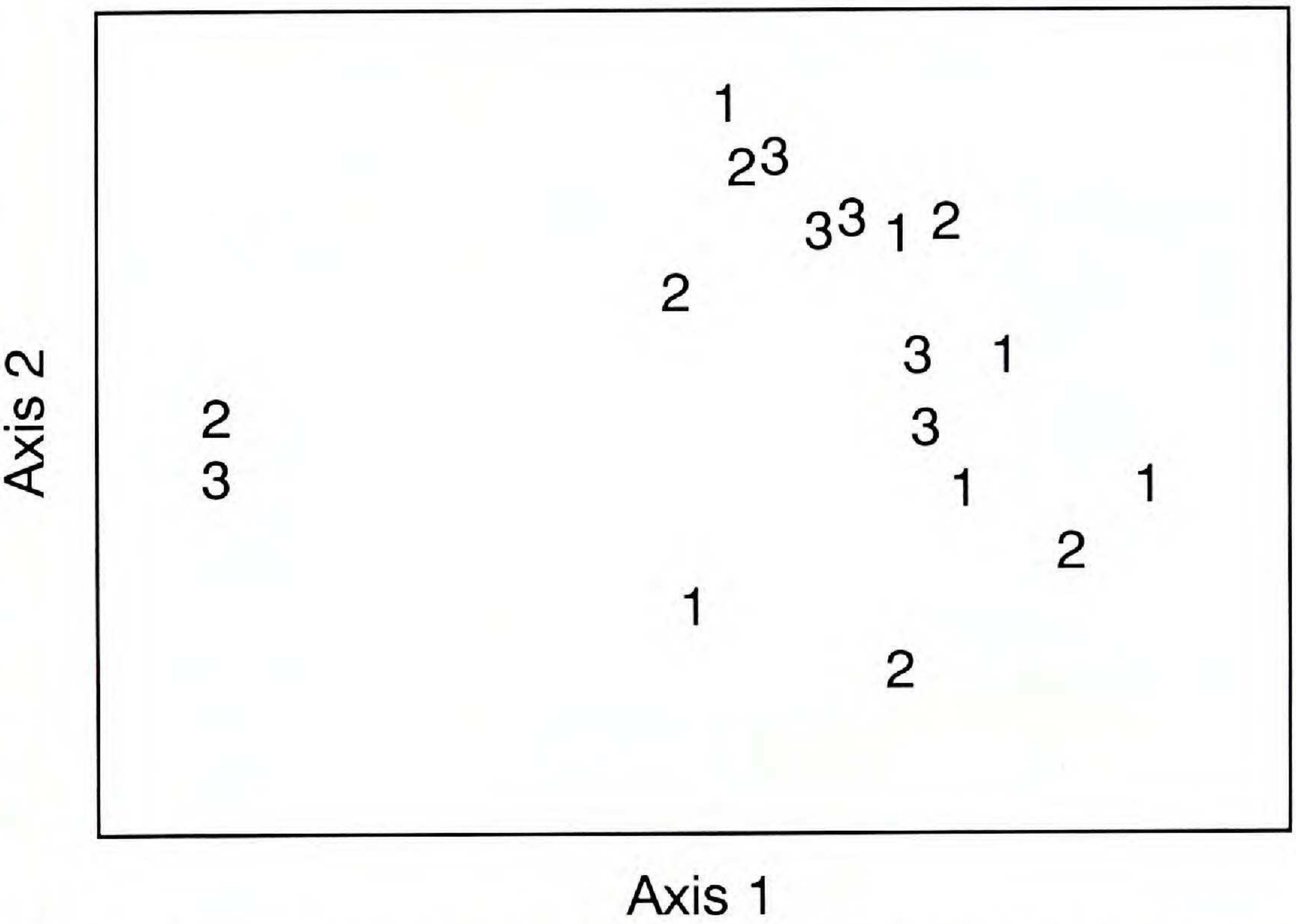

FIG. 7. Results of principal components analysis of cover data for all three canyons. Symbols identify locations of plots by canyon. Lack of segregation indicates that Canyon 2 did not differ in overstory composition from Canyons 1 and 3.

The distribution of *Croton* does not appear to be limited by the availability of sites. Canyon 2, which contained only 3 plants, supported a similar overstory and understory to Canyons 1 and 3. Canyon 2 also contained deep soils and a similar geomorphology to the other two canyons. Likewise, watershed size did not appear to explain *Croton* presence. The only feature that differed among canyons was stream gradient.

Hupp (1988) discusses several ways in which stream channel geomorphology affects vegetation, including fluvial landforms, flood frequency and duration, and stream gradient. It would be consistent with other observations if the steeper gradient of Canyon 2 afforded a less mesic environment that discouraged *Croton* survival. However, fluvial processes in these arid intermittent channels are quite different from those of the eastern floodplain systems that Hupp discusses, and channel gradient is offered only speculatively as a factor explaining *Croton* distribution.

The larger question of how *C. alabamensis* var. *texensis* came to occupy disjunct sites in Alabama and Texas is beyond the scope of this study. Although Ginzbarg (1992) discusses the possibility that the present distribution may be an ice age relict, he suggests that the Texas populations may be more easily explained as the result of relatively recent introduction by long distance seed dispersal by birds. Regardless, it is likely that the disjunct distribution resulted from a prolonged process of migration, colonization, and extinction of many sites. The absence of *Croton* from Canyon 2 may reflect not the lack of available habitat, but the vagaries of colonization and extinction. Perhaps a population once thrived there and has gone extinct, or seeds have, by chance, not recently reached this canyon. More likely, the canyons of the Owl Creek Mountains and similar features of the Edwards Plateau support metapopulations of *Croton alabamensis* var. *texensis*, each subpopulation establishing, thriving, and going extinct only to be replaced somewhere else. Only through repeated observations over long time periods will we understand the process.

Regardless of the limitations on its range within the study area, the behavior of *C. alabamensis* in the Owl Creek Mountains is dramatically different from its behavior in Alabama. Farmer (1962) describes *Croton* as occurring on shallow soils and rock outcrops at mid-slope positions in two counties in Alabama. He describes the habitat as "shallow soil ... on moderately- to steeply-sloping terrain; high temperature of soil and air during summer; intense drought; and freedom from fire." Soil is described as "usually only a few cm thick and seldom more than 1 m thick." In our study site, *Croton* occurs on deep soils on toeslopes and fluvial deposits of canyon bottoms.

The groves in Alabama are "marked by shrub dominance, few or no large trees, and a relative absence of herbs" (Farmer 1962). Occasional plants are found under the forest canopy surrounding the outcrops, but these are considered only "extensions of nearby thickets". This contrasts sharply with *Croton* behavior in Texas. In our study sites, *Croton* occurs as an understory shrub in the company of many large trees and a healthy herb layer.

Farmer considers adaptation to extreme drought to be an important factor in the ecology and distribution of *C. alabamensis* in Alabama (see above). In Texas, however, this species behaves as a drought avoider by remaining in mesic canyon bottoms. Perhaps these differences result only from perceptions relative to annual climate and surrounding vegetation. The 3–5 inches (7–12 cm) of monthly precipitation that Farmer (1962) reports for the "dry" season in Alabama is considerably greater that the 2–3 inches (5–7 cm) recorded for summer months in central Texas (McCaleb 1985). In Texas, where upland vegetation is necessarily drought adapted, a species requiring 7–12 cm of precipitation naturally would be restricted to the most mesic sites.

Another interesting difference between *Croton* behavior in Alabama and Texas regards vegetative reproduction. Farmer (1962) discounts asexual reproduction in *Croton* by stating that "there are no rhizomes or adventitious rootings that result in plant reproduction." In Texas, however, we observed numerous plants that had produced "new" upright shoots through the nodal rooting (layering) of prostrate branches. We did not investigate the degree of connectivity between the layered offspring and the parent plants, but layering appears to be a potential mechanism of asexual reproduction in *C. alabamensis* var. *texensis*.

CONCLUSIONS

The disparate behaviors exhibited by this species over its disjunct range underscore the necessity for site-specific studies prior to making management recommendations. The ecology of *Croton* in Alabama would suggest a conservation strategy that might well be unsuccessful in Texas. The Alabama ecology implies preservation of, and population augmentation into, dry, open, limestone outcrops. This strategy, if adopted in Texas, likely would fail miserably.

We know very little of the disturbance ecology of *C. alabamensis* var. *texensis* in central Texas. The species apparently tolerates some degree of physical disturbance as plants injured or cut off during the pole cutting operation appear to have recovered well. We know nothing, however, of the species' response to fire or soil disturbance. In Alabama, fire is believed to be lethal to *Croton* (Farmer 1962). We saw nothing to indicate a dependence on disturbance for establishment. Conservation efforts, therefore, should focus on maintenance of the undisturbed nature of the mesic forests of the area. Construction of new roads for military training and logging should be discouraged, and old roads should be allowed to fall into disuse. The importance of this plant community has already been recognized for a rare bird; it now appears to be critical to the survival of a rare plant as well.

ACKNOWLEDGMENTS

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APPENDIX 1

Species encountered during line-intercept sampling. Taxonomy follows Correll, D.S. and M.C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation. Renner, Texas.

ACRONYM	SPECIES	FAMILY	GROWTH FORM[1]
ACLI	*Acalypha lindheimeri*	Euphorbiaceae	H
AMAR	*Ampelopsis arborea*	Vitaceae	V
AQHE	Unidentified aquatic emergent		H
ARSI	*Argythamnia simulans*	Euphorbiaceae	H
BULA	*Bumelia lanuginosa*	Sapotaceae	T
CADR	*Calylophus drummondianus*	Onagraceae	H
CAREX	*Carex* spp.	Cyperaceae	G
CEHE	*Ceanothus herbaceus*	Rhamnaceae	T
CELA	*Celtis laevigata*	Ulmaceae	T
CEOC	*Cephalanthus occidentalis*	Rubiaceae	T
CERE	*Celtis reticulata*	Ulmaceae	T
CLTE	*Clematis texensis*	Ranunculaceae	H
CODR	*Cornus drummondii*	Cornaceae	T
COER	*Commelina erecta*	Commelinaceae	H
CRAL	*Croton alabamensis*	Euphorbiaceae	T
CYBA	*Cynanchum barbigerum* var. *texensis*	Asclepiadaceae	H
CYUN	*Cynanchum unifarium*	Asclepiadaceae	H
DITE	*Diospyros texana*	Ebenaceae	T
FRTE	*Fraxinus texensis*	Oleaceae	T
GARE	*Galactia regularis*	Fabaceae	H
GRASS	Various grasses[2]	Poaceae	G
HESP	*Helianthus* sp.	Asteraceae	H
ILDE	*Ilex decidua*	Aquifoliaceae	T
INMI	*Indigofera miniata*	Fabaceae	H
JUAS	*Juniperus ashei*	Cupressaceae	T
JUMA	*Juglans major*	Juglandaceae	T
LEVI	*Lespedeza violacea*	Fabaceae	H
LOJA	*Lonicera japonica*	Caprifoliaceae	H
MEAL	*Melilotus albus*	Fabaceae	H
MIRE	*Mitchella repens*	Rubiaceae	H
MORU	*Morus rubra*	Moraceae	T
OPPH	*Opuntia phaeacantha*	Cactaceae	H
PALU	*Passiflora lutea*	Passifloraceae	V
PAPE	*Parietaria pensylvanica*	Urticaceae	H
PAQU	*Parthenocissus quinquefolia*	Vitaceae	V
PLOC	*Platanus occidentalis*	Platanaceae	T
PODO	*Polanisia dodecandra*	Capparidaceae	H
PRMU	*Prunus munsoniana*	Rosaceae	T
PRSE	*Prunus serotina*	Rosaceae	T
QUMU	*Quercus muhlenbergii*	Fagaceae	T
QUSI	*Quercus sinuata* var. *breviloba*	Fagaceae	T
QUTE	*Quercus texana*	Fagaceae	T
RHAR	*Rhus aromatica*	Anacardiaceae	T
RHCA	*Rhamnus caroliniana*	Rhamnaceae	T
RHTO	*Rhus toxicodendron*	Anacardiaceae	T/V
RHVI	*Rhus virens*	Anacardiaceae	T

APPENDIX 1 *continued*

ACRONYM	SPECIES	FAMILY	GROWTH FORM[1]
RUBI	*Rubus bifrons*	Rosaceae	T/V
SARO	*Salvia roemeriana*	Lamiaceae	H
SMBO	*Smilax bona-nox*	Smilacaceae	V
SOAF	*Sophora affinis*	Fabaceae	T
SOSE	*Sophora secundiflora*	Fabaceae	T
STPL	*Styrax platanifolia*	Styracaceae	T
ULCR	*Ulmus crassifolia*	Ulmaceae	T
UNHE	Various unidentified herbs		H
UNSP	*Ungnadia speciosa*	Sapindaceae	T
VEVI	*Verbesina virginica*	Asteraceae	H
VIMU	*Vitis mustangensis*	Vitaceae	V
YURU	*Yucca rupicola*	Liliaceae	H

[1] G = Grass or grasslike plants; H = Herbaceous plants; T = Trees or shrubs; V = Vines

[2] Grasses encountered during sampling include *Aristida purpurascens*, *Bothriochloa* sp., *Bromus pubescens*, *Dichanthelium acuminatum* var. *implicatum*, and *Glyceria striata*.

APPENDIX 2

Absolute percent cover and frequency of occurrence (no. of transects) of all species encountered during line-intercept sampling. Percent cover is reported for overstory (> 2m) and understory (< 2m) in each canyon. Species are listed in descending order of dominance over the study area, ALLCOV, where ALLCOV was calculated as (overstory cover + understory cover)/3. Plot placement in canyons 1 and 3 was biased by the presence of *Croton* (see text).

	OVERSTORY COVER				UNDERSTORY COVER				
ACRONYM	CYN 1	CYN 2	CYN 3	FREQ	CYN 1	CYN 2	CYN 3	FREQ	ALLCOV
JUAS	51.60	49.67	49.88	18	1.54	3.37	4.67	14	53.58
FRTE	16.50	13.18	26.21	17	3.88	4.93	7.71	18	24.14
QUTE	15.59	29.09	20.11	17	3.69	2.23	0.42	11	23.71
VIMU	9.87	11.68	14.35	13	3.21	3.26	5.29	15	15.89
QUMU	13.39	6.33	8.65	10	0.69	0.18	0.21	6	9.82
RHCA	4.58	2.92	4.87	10	1.21	1.55	7.00	13	7.37
ILDE	5.60	5.62	4.43	13	1.37	3.40	1.17	11	7.19
CRAL	0.22			1	11.24		9.46	11	6.97
ULCR	2.02	4.14	10.67	7		0.75	0.63	3	6.07
JUMA		2.87	8.74	6	0.58		0.04	2	4.08
CELA			9.11	3					3.04
RHTO					2.28	2.90	2.57	15	2.58
GRASS					2.28	2.96	1.90	13	2.38
PRSE	1.95	2.61		6	1.22	1.10		5	2.29
QUSI	3.17	0.33		3	0.83	1.58	0.04	8	1.99
SMBO	0.22	0.08	2.09	5	0.17	1.33	0.68	10	1.52
STPL			1.94	2	0.08	1.05	0.04	3	1.04
CAREX				0.04	2.13	0.90	9	1.02	
BULA	0.14		2.19	3	0.04	0.14	0.11	3	0.88
MORU		0.06	2.39	3					0.81
RHVI		0.58	0.28	2	0.17	0.33	0.72	3	0.69
PLOC	2.03			2					0.68

APPENDIX 2 *continued*

	OVERSTORY COVER				UNDERSTORY COVER				
ACRONYM	CYN 1	CYN 2	CYN 3	FREQ	CYN 1	CYN 2	CYN 3	FREQ	ALLCOV
SOSE		1.21		1	0.04	0.21	0.47	4	0.64
PAQU			0.63	1	0.25	0.63	0.11	8	0.54
COER							1.36	3	0.45
HESP							1.15	3	0.38
VEVI						0.45	0.39	4	0.28
YURU						0.33	0.50	2	0.28
CEOC						0.83		1	0.28
AMAR			0.67	1	0.08		0.04	2	0.26
LEVI						0.43	0.25	2	0.23
PODO					0.29	0.21	0.13	6	0.21
UNSP						0.57		1	0.19
DITE			0.33	1		0.23		2	0.19
RHAR					0.29		0.17	4	0.15
CERE		0.46		1					0.15
SARO						0.30	0.14	5	0.15
INMI						0.42		1	0.14
AQHE					0.42			2	0.14
UNHE					0.08	0.12	0.17	5	0.13
MEAL						0.29		1	0.10
SOAF						0.25		1	0.08
PRMU						0.23		2	0.08
CODR					0.21			1	0.07
OPPH					0.08	0.10		2	0.06
PALU							0.17	1	0.06
CEHE	0.11			1					0.04
GARE							0.08	1	0.03
LOJA						0.08		1	0.03
RUBI						0.08		1	0.03
MIRE							0.08	1	0.03
CLTE							0.08	1	0.03
CYBA			0.03	1			0.04	1	0.02
ACLI						0.05		1	0.02
ARSI						0.05		1	0.02
CYUN						0.05		1	0.02
PAPE							0.04	1	0.01
CADR							0.04	1	0.01

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